

# THE SKULL OF BRACHAUCHENIUS, WITH OBSERVATIONS ON THE RELATIONSHIPS OF THE PLESIOSAURS.

By SAMUEL W. WILLISTON,  
*Of the University of Chicago, Chicago, Illinois.*

The type of the genus and species *Brachauchenius lucasi* Williston<sup>a</sup> is an excellent specimen in the collection of the United States National Museum from the Benton Cretaceous of Western Kansas. The genus is of unusual interest because of several remarkable characters previously unknown among the plesiosaurs, which it possesses, in particular the union of the palatine bones in the middle line, and the very short neck. A second specimen belonging to the same genus, from the Eagle Ford Limestone of Texas, also forming a part of the collections of the United States National Museum, was kindly submitted to me for study by the authorities of that museum, a brief notice concerning which was published in Science for June 19, 1903.

These two specimens supplement each other, the type specimen showing the underside of the skull and the connected vertebral column as far as the lumbar region (Plate XXXIV), while the present specimen permits a thorough examination of the upper part of the skull, and has, also, eighteen of the early vertebræ, and a part of the front paddle. The most careful comparisons fail to discover generic differences between the two specimens, nor can I detect specific differences even. The Texas specimen is partly inclosed in a hard limestone matrix, and it is possible that, when the underside of the skull shall have been cleaned up, specific differences may be apparent, but I do not think so. The specimen is slightly smaller than the type. The Eagle Ford Limestone is known to be an equivalent of the Benton Cretaceous, and I suspect that the immediate horizon in which the specimen occurred will prove to be an exact equivalent of that which yielded the Kansas specimen.

<sup>a</sup> Field Col. Mus., Pub. No. 73, Geol. Ser., II, p. 57; Lucas, Smithsonian Misc. Col. Quart., I, p. 96.

The skull of the Texas specimen is moderately elongated, not nearly so much so as that of *Trinacromerum* or *Polycotylus*, but more so than is the skull of the known species of *Elasmosaurus*. The temporal fossæ are unusually large, the zygomatic bars remarkably slender posteriorly, and the parietal bone is not elevated into a thin, high crest as is the case with the skulls of the genera mentioned, but is low, straight, and obtusely rounded on its upper surface. The teeth are fewer, less elongated than in those genera; they are coarsely striate. All parts of the skull are present, save the anterior portion of the premaxillæ.

*Premaxillæ*.—Of the premaxillæ, the anterior portion has been destroyed, the two posterior teeth on each side only remaining. Since most other forms of plesiosaurs have six teeth on each premaxilla, it is probable that this number was originally present in this specimen, though Andrews gives <sup>a</sup> but five as the number in *Pliosaurus ferox*, a related form. Perhaps two-thirds of the dentigerous portion is missing, and I have so restored the outline of the skull (Plate XXXVII). The facial processes are as in the other forms of plesiosaurs described by me—elongate, parallel processes, with a distinct longitudinal striation, terminating by overlapping the frontals or parietal processes a little in advance of the anterior end of the orbits. Their width throughout is nearly uniform. They articulate, on the outer side of the skull, with maxillæ, frontals and (?) parietals.

*Maxillæ*.—Each maxilla attains its greatest width over the external nareal opening. It is here separated from the premaxillary process by a slender, pointed projection from the frontal or nasal. Between this process and the naris, an elongated tongue-like process extends on the frontal or nasal to a little beyond the posterior end of that opening. Below, the union with the prefrontal begins a little in front of and below the anterior end of the nareal opening and extends downward and backward to the most anterior extremity of the lachrymal. On the right side of the specimen the front part of this suture is apparent, but in the middle of the course there has been an inward bending on the line of the suture. On the left side, however, the maxilla, while a little displaced, has been separated from its contiguous elements, making certain that the infolding has been at the sutural junction. The maxilla lies somewhat over the prefrontal squamately and helps form only the most anterior part of the nareal opening. The maxillary suture turns backward below the lachrymal to terminate acutely a little before the posterior end of the orbit, joining the jugal posteriorly.

(?) *Frontals*.—The bones which I here call the frontals, for reasons given further on, lie at the sides of the parietal prolongations, extending anteriorly as slender projections between the maxillary and pre-

<sup>a</sup> Andrews, Quart. Journ. Geol. Soc., LIII, 1897, p. 177.

maxillary processes already described. Each bone is overlapped in part in front by the tongue-like processes of the maxilla, and I can not be sure whether any part of it reaches the nareal border, though I think not. Near the posterior extremity of this tongue there is a very distinct suture, extending backward and a little outward for a short distance, thence nearly directly backward to a point above the uppermost part of the orbit; on the left side the bone has been separated at this suture. Posteriorly, on the outer side, the bone joins the postorbital for a short distance obliquely; the suture then turns inward to join the parietal transversely. The bone is long, pointed anteriorly, flattened or gently concave above in its middle, united on its inner side in front with the premaxilla, behind with the rostrum of the parietal, posteriorly with the postfrontal and postorbital, on the outer side with the prefrontal. It is of course possible that the bone, as described, is composed of two elements, the most anterior of which would be the nasal, but of such division there is no evidence in this specimen. (See Plate XXXVII, *fr? na?*.)

*Prefrontals.*—The prefrontals are rather broad, irregularly shaped bones, forming the whole of the antero-superior border of the orbits and the posterior inferior margins of the nares. The inner border of each bone, as already described, joins the frontal throughout. Posteriorly, for a short distance, it joins the postorbital, differing in this respect from the prefrontals of *Trinacromerum*. Its orbital border is thin and arched, terminating at the extreme front angle of the orbit. Below, the bone joins the lachrymal by a short suture running forward and outward in continuation of the line of the orbital margin to the maxillary suture, which has been described. Anteriorly the bone is emarginated by the hind border of the nareal opening, the tongue of the maxilla, as described, overlapping it and concealing its extent. The bones are convex and smooth, each pierced by two small foramina. On the left side the bone, while not crushed or distorted, has been separated from the adjoining bones and forced upward somewhat. Inasmuch as its shape and extent on this side agree quite with those of the opposite side, as determined from the sutures, there can be no doubt of its relations and form. There is no indication on either side of a sutural division.

*Parietals.*—The parietal foramen is an elongated opening, oval in shape and about 40 mm. in length. In front of the foramen, the parietals appear to continue forward as an elongated, narrow rostrum, to disappear under the facial extremity of the premaxillæ, divided in the middle by a distinct suture from a little in front of the foramen. The surface on either side of this mesial suture is plane or concave, presenting a number of distinct longitudinal ridges and grooves, which begin near or on the sides of the foramen. The greatest width of these prolongations is at the hind end, where they together measure 50 mm.

Where they disappear beneath the premaxillæ they have a combined width of about 35 mm. On each side the parietal turns downward and slightly outward into a thin descending process or wing, forming the lateral wall of the brain case to a depth of 60 mm. At the anterior inner angle of the temporal vacuity there is a rather strong emargination of this descending wall for the attachment of the epipterygoid, from the upper margin of which a somewhat zigzag sutural line runs upward and then forward to join the extremity of the suture between the prefrontals and frontals. These lines appear to be quite alike on the two sides and since they agree with the sutural divisions in *Trinacromerum osborni* and also with the recognized sutures in the skull described by Andrews as *Pliosaurus ferox*, there can be no question, I think, but that they indicate the divisions between the parietals and postfrontals. Back of the parietal foramen the parietals show no clear indications of a median suture. The part here, for the rather long distance between the temporal vacuities, is obtusely rounded above and nearly horizontal, very unlike the thin, elevated crest of *Trinacromerum*, *Polycotylus*, and *Elasmosaurus*. On the under side the parietals include a deep valley between the lateral walls, a little wider below and meeting in a rounded roof above, for the brain case. This cavity measures over 50 mm. in its greatest width.

The arrangement of the bones in the frontal and antorbital regions, as I have described them, whatever may be their interpretation, doubtless obtains in all plesiosaurs, with minor modifications. Whichsoever interpretation may be finally accepted the arrangement and structure are very remarkable and very unlike what is known in other reptiles. That the bones are nearly or quite as I have described them in this specimen I have no doubt. Andrews, in his figures and description of the skull of *Pliosaurus ferox*, reaches different conclusions and has different interpretations, but I am confident that, if his specimen be studied in the light of the information furnished by the present one, other conclusions and other interpretations will be reached. A positive suture has never been detected separating the median bones in front of the pineal foramen from the parietals. Owen, it is true, thought he detected such a suture in a species of *Plesiosaurus*, and Andrews thought there was one in his *Pliosaurus ferox* specimen, though he adds that the parietals are probably ankylosed with the "frontals." I have been unable to distinguish such a suture in four well-preserved skulls of as many different genera studied by myself. In the specimen of *Trinacromerum osborni* studied by me, while the adjacent sutures are all clearly indicated, save such as were obliterated by crushing, the very narrow prolongations in front of the foramen have no trace whatever of a distinguishing suture, either on the upper or the under side. I believe them

to be merely exogenous processes from the parietals, produced forward to meet the extraordinarily elongated premaxillary processes.

If such be really the case, the bones on their outer sides must of course be the frontals, and, as frontals, they occupy their normal relations with the adjacent bones, save only the parietals, articulating behind with the postfrontals, in front exteriorly with the prefrontals, anteriorly with the maxillæ and premaxillæ. If the median bones be really the ankylosed frontals, then these bones must be the nasals. As such, however, their relations would be most extraordinary, the only instance in comparative osteology where they articulate with the postfrontals and postorbitals.

Possibly the same causes which have prolonged so far backward the premaxillaries may have caused a posterior displacement of the nasals. In any event I feel sure that the bones on the outer sides of these, the supposed supraorbitals, the ones bordering the orbits and reaching to the nares, are the real prefrontals. As such their position and relations are not extraordinary. As supraorbitals they are quite indefensible.

If the former interpretation be correct, that the parietals have excluded the frontals from contact in the middle line, the nasals are wanting in the plesiosaurs. If the latter interpretation is correct, then all the elements of the normal reptilian skull are present, but the nasals have become abnormal in position and relations. I do not know how the problem can be settled, unless, indeed, some favorably preserved specimen may disclose an actual suture in front of the parietal foramen.

*Lachrymals.*—The lachrymal is an elongate bone forming the lower anterior half of the orbital margin. Its sutural union with the prefrontal is very evident on each side; the suture between it and the maxilla is perhaps not wholly free from doubt in this specimen, though there can be little possibility of error, the indications of the two sides agreeing as they do. The bone joins the jugal behind by an oblique suture; the maxilla in the middle below; and the prefrontal anteriorly, as already described. Inasmuch as these relations seem to be quite the same as those described by Andrews in *Pliosaurus ferox*, I think that the presence of a lachrymal as a distinct bone in the plesiosaurs may be finally set at rest. In the skull of *Trinacromerum osborni*, previously described, there is a pointed process of bone which has the same relations with prefrontals and maxillæ, but not with the jugal. I could not detect a suture separating it from the maxilla. Neither is it probable that the lachrymal in *Elasmosaurus snowi*, which must resemble that of *Trinacromerum*, articulates with the jugal.

*Postfrontals and postorbitals.*—The postfrontals and postorbitals I believe are distinct bones in this specimen. The parieto-post-

frontal suture I have already described. A suture quite as evident on each side runs obliquely outward from the hind end of the frontals or nasals, and then turns downward, about as figured by Owen for *Plesiosaurus*. The postfrontal, as thus defined, joins the parietal and touches the epipterygoid internally, the frontal anteriorly, and the postorbital exteriorly. The postorbital articulates with the prefrontal anteriorly, the postfrontal on the inner side, and, by its anterior angle, the so-called frontal; and the jugal exteriorly. The two bones, seen from behind, present a broad, nearly vertical wall, deflected somewhat anteriorly below, and ending in a thin, sharp, nearly horizontal margin, continued from the epipterygoid notch to the jugal. The orbital border of the postorbital is thinned, somewhat serrated, and concave. The temporal border above is sharp and angular, curving downward to terminate in the thin upper margin of the zygoma. The bone outwardly is massive and strong, ending in a horizontal suture, which is nearly continuous with the lower border of the orbit and the upper front border of the zygoma.

*Jugals.*—The jugal differs considerably from that of other forms of plesiosaurs known to me. The sutures distinguishing it from the postorbital, lachrymal, and maxilla are very clear, as I have described and figured them. That uniting it with the squamosal is doubtful. On the left side the bone has been separated very cleanly from the matrix, and is in a beautifully undistorted condition. A little back of the hind border of the postorbital there are, near the middle of the jugal, the orifices of two or three malar canals. These canals are very characteristic of the plesiosaurs, and usually open near the squamoso-jugal suture, but there is not the slightest indication of such a suture here. These canals, piercing the jugal, enter the orbit near its lower posterior corner. In the orbit the jugal turns inward for a considerable distance, forming a bowl-like floor posteriorly; its inner border I can not trace.

Describing the zygoma as a whole, it has a somewhat thickened upper border in front, thinned below. The arcade diminishes rapidly in width, chiefly at the expense of the lower part, to beyond its middle, where its width is less than one inch, and the bone is thin and weak. At this place the arch, on both sides, shows an oblique fracture, which may, possibly, represent the squamosal suture, though I am very doubtful. I have indicated this possible suture by dotted lines in the drawings. The squamosal behind broadens to a width of about two and a half inches where it joins the quadrate, and is thicker here, the upper border ascending rapidly; the lower border is concave. The zygoma is very remarkable for its attenuation posteriorly, leaving a large open space above the posterior part of the mandible in front of the articulation. I can conceive of the complete erosion of the bar here, as occurs in some turtles, leaving the temporal vacuity broadly

open on the sides. It would seem that the chief support for the mandibular muscles must have been on the sides of the parietals and the stout postfrontals and postorbitals.

The limits of the squamosal above can not be determined, owing to the erosion of the specimen, as indicated in the drawing. The parieto-squamosal arch is, however, quite stout, narrowed anteroposteriorly near its upper part. The massive quadrates are exposed below on the outer side and behind. Further information concerning the occipital region can not be had until the matrix has been removed; the anterior cervical vertebræ are crowded into this space.

At the bottom of the large temporal vacuities the supraoccipitals, exoccipitals, petrosals, and stapes were found more or less disarticulated and separated. The larger part of the exoccipital is seen somewhat removed from its relations to the stout supraoccipitals. Its anterior, cranial surface presents a deep pit and marginal sutural surfaces, completed by union with the supraoccipital and petrosal. The paroccipital process is rather slender, directed downward, outward, and backward in life, with its distal extremity flattened and apparently spatulate, for union with the upper end of the quadrate, as described in *Trinacromerum osborni*.

*Petrosals.*—The petrosal is a peculiar bone. That of the left side has been wholly freed from its matrix; on the right side it lies with its free, convex, outer side exposed near the front border of the temporal vacuity. Exteriorly the bone is nearly evenly and smoothly convex, shell-like. The inner side I have figured in Plate XXXV (*pet*), natural size. Its precise mode of union with its two contiguous bones can not be determined. Its two diverging canals doubtless lead into the supraoccipital and exoccipital sinuses or semicircular canals, as I have found them in *Trinacromerum osborni*. The greater part of the bone is deeply and smoothly excavated for the internal ear, leaving a free border for the petrosal part of the large foramen ovale. The excavation is deep and large for the size of the skull, much larger proportionally than in the mosasaurs.

*Stapes* (?).—A small and peculiar bone, lying apparently nearly in position in the matrix on the right side, I can determine only as a stapes, a bone hitherto unknown among the plesiosaurs. It is a short, stout bone, a side view of which is shown in Plate XXXV (*st*) natural size, not unlike a human metatarsal, though less slender, with an attenuated, cylindrical shaft, and an articular expansion at either end. What I believe to be its proximal end, from its position in the matrix, presents a hemispherical articular surface, bounded by a shelf-like ridge, as though for articulation in a foramen. The other extremity is obliquely expanded, concave somewhat from side to side, smooth, and with a partial longitudinal ridge near one side. The extremity of the bone has been broken away.

Where the external ear was located is a puzzle. In all probability there was an external tympanic closed membrane, as in the turtles. The shortness of the stapes, if stapes this bone be—and there is no other place in the skeleton where it can be located—must mean an external surface close to the median line of the skull. There are no indications of an otic foramen or notch anywhere about the quadrate that I have discovered in this or other specimens of plesiosaurs. Dollo has ventured the opinion, from the thickness of the preserved cartilage about the external ear in certain mosasaurs, that they, or certain types of them at least, were deep-sea divers, from the resemblance in the structure to that of the cetaceans. This ear cartilage is very abundant and very thick in *Platecarpus* and *Tylosaurus*, less so in *Clidastes*. No calcified cartilage of any kind have I ever observed anywhere in the skeletons of plesiosaurs, so that any inference as to the habits of the plesiosaurs from its absence about the ear would not be legitimate.

*Paddle*.—A part of a paddle, evidently an anterior one, shown in Plate XXXVI, was found in this specimen lying closely upon and across the face of the skull. Not much information as to the generic or specific characters of the form can be deduced from it, but I give, nevertheless, a good photographic view of the specimen. The limbs were evidently not of the slender type of the elasmosaurs, but whether or not there was a duplication of the epipodials can not be determined.

*Vertebrae*.—The remains of twelve cervical and six dorsal vertebrae are preserved in the limestone matrix back of the skull. They agree in all respects with the vertebrae described by me in the type specimen of *Brachauchenius lucasi*, save in their slightly smaller size. The cervical series is connected, as are also five of the dorsals, which are curved forward reversed by the side of the cervicals. Doubtless the specimen originally was composed of a large part, perhaps the larger part of the skeleton, though only the single block containing the skull and vertebrae and the attached paddle was secured by the collector. At the angle of the vertebral series one or two may have disappeared, but probably not more. I have every reason to believe that the number of the cervicals is the same as in the type, namely, 13. The cervicals measure, in length, beginning with the axis: 25, 25, 25, 25, 28, 28, 30, 33, 35, 40, 40 mm. The dorsals preserved: 45, 50, 60, 60, 60 mm. The centra of the dorsals are smoothly rounded on the under side, without excavations or vascular foramina, resembling dinosaur vertebrae so closely that it would be difficult to distinguish their centra if preserved singly. The cervical ribs are single-headed, with not the least indication of division.

The total length of the skull, with the missing premaxillary portion estimated, is about 0.80 m., the width at the posterior part of the orbits 0.35 m. The length of the type specimen is about 0.90 m.; the width proportionally the same.



*Relationships of Brachauchenius.*—The most distinctive characters of the genus are found in the broadly united palatines, the broad union of the pterygoids posteriorly, the short, deep-set interpterygoidal vacuities, the ridge-like buttresses of the pterygoids, the remarkably small number of the cervical vertebræ, the absence of vascular foramina on their under side, the single-head cervical ribs, etc. The dorsal surface of the skull has a remarkable resemblance to that of *Pliosaurus ferox*, as figured by Andrews. Andrews assumed that the palatines in his specimen were separated by the pterygoids throughout, but expressly says that indications of the palatine relations posteriorly are wanting. I have scarcely a doubt but that they will be found to have the same structure as in *Brachauchenius* in better preserved specimens of the genus.

Much stress has been placed upon the palatal structure in the reptiles as indications of phylogenetic relationships, but I have never had a great deal of faith in the stability of these parts. Here we have the union or separation of the palatines in the same order. The general shape of the skull, the depressed parietals, and, I am confident, the relations of all the other bones of the upper side of the skull, are all nearly alike in *Pliosaurus* and *Brachauchenius*. Furthermore, in the reduced number of the cervical vertebræ in the two forms, 18 or 20 in the older, 13 in the younger, we have a genetic resemblance, I believe, one that strengthens my assumption that the shortened neck in the later forms is not a primitive character, but a degenerate one, one that has been acquired in more than one phylum. Indeed, so far as all these characters of the skull go, in the probability that the arrangement of the skull bones will be found essentially alike in the two genera, I should hesitate to separate the two types generically, were it not for the cervical ribs, single-headed in *Brachauchenius*, double-headed in *Pliosaurus*. The character of the cervical ribs has been considered as of more than generic importance, Seeley even proposing an ordinal subdivision based upon the divided or undivided neck-ribs. Here, too, I believe that the fusion of the imperfectly differentiated heads is a feature common to more than one line of descent, and is of no more than generic importance. It is a fact that all known American Cretaceous plesiosaurs have cervical ribs with undivided heads, and that is probably the case with all Cretaceous forms, as it is also with the known American Jurassic ones. Double-headed ribs are a primitive character confined to the early forms, for the most part.

In conclusion, I would suggest that the family Pliosauridæ be maintained, based upon the common characters apparent or probable in *Pliosaurus* and *Brachauchenius*.

The characters of *Brachauchenius*, so far as they are now known, I give as follows:

*Brachauchenius.*—Mesocephalic. Teeth not more than 20 in each

maxilla, strongly ridged and anisodont. Parietals rounded and obtuse above, not elevated into a crest. Temporal vacuities large; zygomatic bars slender posteriorly. Pterygoids broadly united in the middle behind; the interpterygoidal vacuities short, at the bottom of a depressed pit. No palatine foramina. Palatines broadly united in the middle in front of the pterygoids. Cervical vertebræ 13 in number, smoothly rounded below, without vascular foramina, shallowly concave at extremities; cervical vertebræ broader than long; cervical ribs single-headed. Benton Cretaceous of Kansas and Texas.

*Relationships of the Plesiosaurs.*—In the attempt to reach some definite conclusions as to the habits of the plesiosaurs, I gave<sup>a</sup> five years ago the following list of adaptive characters in aquatic, air-breathing vertebrates:

1. Elongation of the head, with attenuation of the facial region.
2. Elongation of trunk and tail, but especially the latter, with progressive weakening of the zygapophysial articulations posteriorly.
3. Shortening of the neck.
4. The acquirement of a caudal fin.
5. The acquirement of sclerotic plates.
6. Recession of the external nares.
7. Absence of the sacrum and the absence or progressive obsolescence of the sternum.
8. Greater slenderness and smaller size or loss of the hind limbs.
9. Hyperphalangy and hyperdactyly.
10. Smoothness of the skin.
11. Sponginess of the bones of the skeleton.
12. Increase in number and decrease in size of teeth.

The exceptions which the plesiosaurs present to these adaptations are:

1. Elongation of the neck, with increase in number of vertebræ.
2. Shortening of tail and body, and the flattened, depressed form of the latter.
3. The presence of a well-defined sacrum of three vertebræ.
4. The somewhat greater slenderness of the hind limbs, but with little or no decrease in effectiveness as propelling organs.

In these exceptions the plesiosaurs agree with the marine turtles. In the tail-propelling, aquatic vertebrate the propodial bones are invariably shortened, as for instance in the Cetacea, Ichthyosauria, Pythonomorpha, and the front legs of the Thalattosuchia, and the limbs become merely equilibrational organs in direct proportion to the effectiveness of the tail as a propelling organ. Experiments on fishes show that the loss of the paired fins does not impair the swimming powers of the individual, but does require the constant vibrational use of the tail in the preservation of the equilibrium, while the

<sup>a</sup> Kansas University Science Bulletin, I, 1902, p. 259.

loss of the caudal fin results in the total disability of the animal. In animals propelling themselves wholly or chiefly by the aid of the limbs the propodials are not shortened, but are, on the contrary, elongated, as in the plesiosaurs and marine turtles. The reason is obvious: The propodials become elongated handles of oar-like organs, of which the blades are formed by the progressively widened epi-, meso-, and metapodial elements, and the phalanges. The front limbs of the plesiosaurs are always broader and stronger, but not longer than the hind ones. The front legs of the marine turtles are not only broader and stronger, but also longer than the hind ones, though the latter have by no means lost their effectiveness as propelling, or, more probably, guiding organs. The connection of the hind limbs of the plesiosaurs with a well-developed sacrum of three vertebræ conclusively proves the propelling function of these limbs, if such proof were not abundantly furnished by the limbs themselves.

We have, then, certain marked resemblances in the form and mode of progression between the plesiosaurs and turtles, as contrasted with the tail-propelling type presented by the ichthyosaurs, mosasaurs, and thalattosuchians; and Fraas uses<sup>a</sup> this resemblance as a support for the diphyletic grouping of the reptilia by Osborn into the Synapsida and Diapsida, the former having the oar-propelling type, the latter the tail-propelling type. But the argument is fallacious; the resemblances in mode of progression and bodily form no more imply a common phyletic origin than do the much more marked resemblances of the ichthyosaurs and dolphins.

It is chiefly because of the external resemblances of form and similarity in mode of locomotion in the water that it has been generally and indefinitely assumed, from Buckland's time to the present that the plesiosaurs were related to the turtles. How well this hypothesis is sustained by the internal structure may be shown by the following comments:

In addition to external resemblances and undoubted similarity in habits of life, two other characters have been often cited as evidence of relationship between these two orders—the epiphysial mode of ossification of the propodials (or rather of the humeri, since there is no evidence yet that the femora have the peculiar “epiphyses”), and the fusion of the procoracoid with the scapula. As to the first of these assertions, recent careful investigations by R. Moodie conclusively prove that the turtles do not have true epiphyses, and as was long ago stated by Dollo, and recently confirmed by Mr. Moodie, the lizards do have, many of them, at least, distinct terminal bony epiphyses on their long bones. The mode of ossification of the humerus of the plesiosaurs is most extraordinary, without known parallel among reptiles, or mammals either, so far as that is con-

<sup>a</sup> Jahresheften d. Vereins f. vaterl. Naturkunde in Württemberg, 1905, p. 363.

cerned.<sup>a</sup> The presence of "epiphyses" forming nearly the whole of the humerus, their apices separated in the middle of the bone by perforating canals extending through the shaft of the bone, is utterly unlike anything that has been observed in turtles or any other reptiles at any stage of their existence. I trust that the myth of epiphyses as an evidence of relationship between the turtles and plesiosaurs may not reappear again.<sup>b</sup>

As to the structure of the scapula, all students of the plesiosaurs are now agreed that the procoracoid does not unite with the scapula, whatever may be the case in the turtles (where it is equally improbable). The presence of a distinct foramen in the coracoid of many plesiosaurs, or its deep emargination posteriorly, points, I think, to a normal reptilian manner of development of this bone. The tri-radiate structure of the scapula is simply a parallel character, brought about by the same causes which have produced the enormous development of the coracoids, a structure absolutely lacking in the earlier and simpler nothosaur type, where it would confidently be expected were the orders genetically allied.

Whatever of resemblance there may be in the form and habits of these two orders of animals has been due solely to parallel evolution, to similar aquatic adaptations. In their internal structure they are really remote from each other, and neither could have been derived from the other type, not even in a remotely antecedent stage. The turtles have a stegocrotaphous skull, unlike all other reptiles save the Cotylosauria, Procolophonia, etc. The plesiosaurs have a large temporal vacuity, larger indeed than is to be found in any other reptiles of the therocrotaphous (I coin the word) type. Leaving out of account adaptive characters, we have the following most important differences in the structure of the two orders: The turtles lack the lachrymal, postorbital, and transverse bones, all well developed in the plesiosaurs. They have a distinct opisthotic, wanting in the plesiosaurs, and a large quadratojugal, probably wholly wanting in the plesiosaurs. The plesiosaurs have a large pineal foramen, wholly

<sup>a</sup> See Williston, Field Columbian Mus. Publ. No. 73, p. 73.

<sup>b</sup> In the pigeon "at four days there are two cones of gradually ossifying cartilage, the apices of which are close together in the middle of the bone, at the point where the primary center of ossification occurred, while the bases, quite unossified, form the articular ends. These two cones are ensheathed by a layer of periosteal bone, which of course is thickest opposite the ends of the cones, and thins off as the two extremities are approached. . . . These two cones probably represent the so-called epiphyses of the Plesiosaurus. I have not been able to find that this reptile possessed anything corresponding to true epiphyses." (Parsons, Jour. Anat. and Physiol., XXXIX, 1905, p. 403.) The figure of the bird humerus, given by Parsons, strikingly resembles the ossificatory plan in the plesiosaurs, save that the latter in the early stage has perforating canals through the rudimentary medulla. These observations of Parsons, seen by me for the first time since the above was in type, effectually dispose of the whole matter of turtle relationships in the manner of ossification of the long bones.

wanting in the turtles. The turtles have a single, unpaired, true vomer and no prevomers; the sauropterygians have large prevomers and a small or no true vomer. A large interpterygoid vacuity is present in the plesiosaurs, wanting in the turtles. Furthermore, the turtles have still preserved the primitive hypocentral mode of attachment of the thoracic ribs, while the single-headed thoracic ribs of the plesiosaurs are attached high up on the extremities of the diapophyses, and this character can not be ascribed to aquatic adaptation, I think, since the ichthyosaurs and mosasaurs have preserved their early pleurocentral attachment of these ribs.

And one is welcome to all the resemblances that may be found in the vertebræ, girdles, and limbs. I repeat, there is only a remote relationship between the two orders in osteological structure. The plesiosaurs could not have been derived from any ancestors that might by the widest stretch of imagination be called Chelonia, or Chelonia-like. Nor could the turtles have come from any forbears even suggesting the sauropterygian structure.

I am still strongly of the opinion that the Sauropterygia were derived from a primitive therocephalian ancestry; while I am firmly of the opinion that the turtles have had a quite independent origin from some primitive cotylosaurian, like the Chelydosauria, as Case has forcefully shown. The turtles occupy a phylum distinctly their own, no more intimately related to the plesiosaurs than they are to the ichthyosaurs or rhychocephalians. I can not accept the contention of McGregor that the Ichthyosauria had a primitively saurotaphous (I need not apologize for the word) type of skull, but would rather believe that they, too, enjoyed a genealogical line all their own from the most primitive type of reptiles, and that they should no more be grouped with the dinosaurs and crocodiles than with the plesiosaurs and theriodonts.

#### EXPLANATION OF PLATES.

##### PLATE XXXIV.

*Brachiauchenius lucasi*, type specimen in U. S. National Museum. After Lucas. (Plate from Vol. I, Quarterly, Smithsonian Misc. Col.)

##### PLATE XXXV.

Skull of *Brachiauchenius*, U. S. National Museum Collection, from Eagle Ford Shales of Texas. One-fourth natural size. *Exo*, exoccipital; *Pet*, petrosal; *St*, stapes.

##### PLATE XXXVI.

Part of front paddle of *Brachiauchenius*, Texas specimen, one-half natural size.

##### PLATE XXXVII.

Restored outline of skull of *Brachiauchenius*, Texas specimen, one-half natural size. *Ang*, angular; *Ep*, epipterygoid; *Fr?*, frontal; *Na?*, nasal?; *J*, jugal; *La*, lacrymal; *max*, maxilla; *na*, external naris; *Pa*, parietal; *Pf*, parietal foramen; *Pfr*, postfrontal; *Po*, postorbital; *Prf*, prefrontal; *Pmx*, premaxilla; *Q*, quadrate; *Sq*, squamosal; *Sur*, surangular; *Tv*, temporal vacuity.